A Report on the Feeding of Dendronotus iris on the Anthozoan Cerianthus sp. from Monterey Bay, California

BY

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(Plates 55 to 57)

INTRODUCTION

Dendronotus iris Cooper, 1863, is found subtidally throughout the year in Monterey Bay, California, feeding on the anthozoan *Cerianthus* sp. The association which has evolved between the two animals has not been previously described and might be viewed as a simple predator-prey relationship, were it not for the fact that *D. iris* crops but does not, or perhaps can not, destroy the *Cerianthus*. After consuming only a very limited part of this prey, the nudibranch moves to other *Cerianthus* individuals for further feeding. It is rare in nature to find different species of similar size where this type of "conservation" exists. This and other factors point to a delicate interrelationship which could be said to approach parasitism. The present study is a description of some of the behavioral aspects of this association.

METHODS AND MATERIALS

Observations and experiments, using SCUBA gear, were made off the seaward side of the United States Coast Guard Breakwater (hereafter referred to as the 'Breakwater') at the southwest end of Cannery Row, Monterey, California, from 1965 to 1969, at depths of 50 to 60 feet.

A rectangular quadrant area of $3 \text{ m} \times 33 \text{ m}$ was marked off on the flat mud bottom running parallel to the base of the Breakwater. The protected edge of the study area was bordered by large boulders which form the Breakwater. The study area contained 193 *Cerianthus* individuals. Notes were kept on this population, which remained stable, from October 5, 1968 to December 31, 1968. *Cerianthus* grow densely the length of the Breakwater, concentrated in a narrow strip close to its base.

An equal area directly to the seaward of the study area supported only 11 animals.

Cerianthus were isolated on the bottom in cages made of aluminum frame and screening, held in place by aluminum stakes pounded into the soft substrate.

Specimens of *Dendronotus iris* were of 2 distinct color phases. Most had salmon-red bodies, and cerata and branchial processes with orange ends, the tips of which were white. In others the bodies were much lighter in color, light milky purple with light orange processes, tipped with white. The cerata and branchial processes of both color phases sometimes had smaller purple side branches. The largest specimen was 20 cm long. There seemed to be no relationship between color and size.

OBSERVATIONS

Feeding

Dendronotus iris feeds on Cerianthus tentacles. Over a period of 2 months, 2 to 6 nudibranchs were found on each dive in the study area. These were generally in various attitudes of feeding. Because the average Cerianthus tube projects above the substrate about 15 cm (larger specimens to 21 cm), the nudibranch must climb the tube to reach the tentacles. Two methods of feeding were recorded.

The first approach is used mainly by smaller (5 cm or less) *Dendronotus iris*. The nudibranch climbs the tube and slowly enters the rim of marginal tentacles. At this point *Cerianthus* reacts by:

- a. retracting swiftly and directly down its tube, D. iris often climbing into the tube after the tentacles, or
- b. allowing the nudibranch to crawl in among its partially withdrawn tentacles and feed (Plate 55, Figure 1), or

c. curling the ends of its marginal tentacles into tightly coiled "pigtails," in which case the nudibranch crawls back down the outside of the tube and leaves. This is uncommon and has only been seen twice (Plate 57, Figures 5 and 6).

The second approach, in which the nudibranch is pulled into the Cerianthus tube, is common among larger nudibranchs. The nudibranch crawls up the outside of the tube to within 35 mm of the lip. When one of its spreading crown papillae, which form branched sheaths surrounding retractile rhinophores, touches a tentacle, an immediate and obvious stimulation of the nudibranch takes place. The nudibranch raises the front part of its body from the surface of the tube, arching the head back as though peering up at the tentacles spread out above. At the same time the mouth is thrust out baring large, fleshy lips, and elongating the otherwise rather thick and snubbed anterior end. Thus extended, the nudibranch makes a sudden upward thrust with the anterior part of its body, almost always catching one or more of the marginal tentacles in its mouth (Plate 55, Figure 2). The lips of D. iris form a vertical groove in which the tentacle is aligned. As well as aligning the tentacle for the jaws to close on, the lips seem to orient the nudibranch in relation to the position of Cerianthus. Sometimes after brief lip contact with the distal end of a tentacle, the strike is made at the tentacle base. Dendronotus iris then gives a violent tug backwards, causing Cerianthus to retreat quickly into its tube. The nudibranch hangs onto the tentacles with its jaws. In most instances the force of the retreating tentacle(s) pulls the nudibranch from its hold on the outside of the tube over the lip, head first, down into the interior where it disappears completely from sight (Plate 56, Figure 3). The nudibranch stays inside the tube to complete feeding. Time spent inside tubes varied from 20 minutes to over $2\frac{1}{2}$ hours.

Large *Dendronotus iris* sometimes miss in the attempt to bite *Cerianthus* tentacles. The *Cerianthus* retract and the top of the tube often collapses by folding, or the end pinches closed. If this happens, most *D. iris* do not, or can not, enter. If the tube remains open, the nudibranch climbs in and feeds. To isolate the effect of *Cerianthus* tentacles on *D. iris*, marginal tentacles were cut from live

Cerianthus. Three or 4 of these tentacles were held with a test-tube holder so that the distal ends were free. A D. iris was found crawling across the substrate (not on Cerianthus). Cerata touched by anemone tentacles showed no reaction. The tentacles were touched to the crown papillae. As soon as contact was made, the Dendronotus began extruding the mouth area (as described above) and arched back the head exactly as it does when on a Cerianthus tube. It extended its anterior end and made a lunge forward, biting with its jaws as though biting at tentacles.

A Dendronotus iris was placed on the tube of a retracted Cerianthus. No tentacles projected from the tube. When the crown papillae of D. iris were touched briefly with the testing tentacles, D. iris reacted exactly as above, this time making lunges toward the top of the tube, striking several times with its jaws.

During one observation period 3 Dendronotus iris struck at, but did not successfully hold onto Cerianthus tentacles. All 3 Cerianthus retracted and the nudibranchs left. Two of the Cerianthus came out again within 2 hours. The third remained within its tube for over 8 hours. None of the 3 had its tentacles damaged by the D. iris encounter. Sightings of such retractions and the re-emergence of Cerianthus varied from 1 hour and 20 minutes to over $8\frac{1}{2}$ hours.

Quiescent Posture

Dendronotus iris is sometimes seen in a "sleeping" or quiescent posture. In this posture a nudibranch clings to the outside of a tube near the top, attached by the posterior end of its foot. The anterior part of the foot is unattached, and the back is arched. The head is held in an upright position, and the nudibranch does not move, except to sway back and forth with the currents. When taken off the tube in this state, a nudibranch took a few seconds to become active again. One *D. iris* maintained the quiescent posture for over 8 hours.

Whether the quiescent posture represents a digestive period, a recovery period, or otherwise, I cannot say. Some nudibranchs crawl off the *Cerianthus* immediately after feeding, some remain on the tube to lay eggs, and others assume the quiescent posture.

Explanation of Plate 55

Figure 1: Dendronotus iris feeding among extended Cerianthus sp. tentacles

Figure 2: Dendronotus iris on Cerianthus sp. tube. Dendronotus iris has just made a sudden upward thrust, baring large fleshy lips which make contact with a Cerianthus sp. tentacle.



Figure 1



Figure 2



Escape

When Dendronotus iris is handled, it often swims by means of heavy side-to-side gyrations of the body (Plate 56, Figure 4). This motion in light surge conditions, normal off the Breakwater, does not appear to orient the nudibranch in a positive direction, but seems to be an escape response to take it off the substrate. I did not test this swimming reaction in the laboratory or under controlled conditions. Agersborg (1922) states that swimming is Dendronotus giganteus' most common mode of locomotion and assumes that it is pelagic in habit (D. giganteus O'Donoghue, 1921 is synonymized with D. iris by MacFarland, 1966). Dendronotus iris' swimming activities in Monterey seem restricted to escape reactions only. Once off the bottom, D. iris is at the mercy of water movement until it comes in contact with something solid for a new foothold.

The active reef predator, Pycnopodia helianthoides (Brandt, 1835), is often seen on the floor of the bay. This sea star is able to excite Dendronotus iris into a violent type of swimming escape response. In one observation, the anterior end of D. iris was inside the tube of Cerianthus with only the posterior end visible. Pycnopodia helianthoides was placed 15 cm from the base of Cerianthus. The sea star approached, one ray slowly extending towards the nudibranch. As soon as contact was made, the nudibranch backed out of the Cerianthus tube, released itself from the tube, and started gyrating. Water currents carried it away. Twenty similar experiments with P. helianthoides and different D. iris resulted in the same immediate escape reaction.

The bat star, Patiria miniata (Brandt, 1835), often seen on Cerianthus tubes, will cause a slower and not so violent swimming reaction of shorter duration. I have never seen a sea star of any kind attack Dendronotus iris in the field under natural conditions. It is of interest that when a ray of Pycnopodia helianthoides is touched to the Cerianthus, the sea star withdraws its ray.

Dendronotus iris is affected adversely when it comes in contact with the anemone Tealia sp. which is found among the Cerianthus beds. I have guided several swimming D. iris onto Tealia. The tentacles immediately adhere to the D. iris and pull it toward the mouth where it disappears into the gullet. Usually a slight escape response is seen, but the response is weak and ineffective, as though the nudibranch were partially paralyzed. When a single Tealia tentacle was touched to D. iris, the nudibranch turned aside and crawled in the other direction.

Reproduction

Dendronotus iris lays ringlets of white eggs on the outside of Cerianthus tubes, attaching them at a point high off the muddy bottom. This position may help in avoiding predators, and additional protection may be gained by proximity to the anthozoans' tentacles. Eggs have been seen during most of the months of the year and at one time adults of all sizes are found. Copulation takes place on the Cerianthus tube or on the mud bottom. Copulation between the two color phases of D. iris is common.

Locomotion

The expansive foot of *Dendronotus iris* is elongate, flattened, and muscular. It is highly ciliated and has good adhesive qualities (Agersborg, 1922). The foot is adapted for travel on sand or mud bottom, and for clinging to *Cerianthus* tubes in surge conditions.

Movements of crawling *Dendronotus iris* were traced. Animals were seen to crawl past *Cerianthus* in what seemed to be random directions. However, when crawling away from *Cerianthus* beds, nudibranchs were seen to reverse their direction. Whether or not a specific chemical attractant or other signal is involved needs to be explored.

Tentacle Damage

The foraging habits of *Dendronotus iris* are such that it goes from one *Cerianthus* to another. After being attacked, the anthozoan stays within its tube. *Cerianthus* near feeding *D. iris* are often retracted, as though having been recently disturbed, even though 90 to 95% of the *Cerianthus* outside the immediate area may be in the expanded state. Repeated examinations of *Cerianthus* tentacles after *D. iris* has fed on them, have shown only minor damage with but 2 to 10 tentacles missing.

To get an indication of damage a single nudibranch might do to a *Cerianthus* if both were confined, 2 nudibranchs over 16 cm in length were kept in the field without food for 48 hours. Cylindrical screen cages 48 cm high by 30 cm diameter were placed over separate *Cerianthus*. One "starved" nudibranch was placed in each of the 2 containers. Within 15 minutes, both nudibranchs had climbed the *Cerianthus* tubes, attacked the tentacles, and were pulled inside the tubes, where they remained.

Four days later both nudibranchs were on the bottom of the cages. When the cages were removed the nudibranchs crawled away to feed on other *Cerianthus*. The 2 test